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BIOLOGY AND IMMATURE STAGES OF SNAIL-KILLING FLIES BELONGING TO THE GENUS *TETANOCERA* (INSECTA: DIPTERA: SCIOMYZIDAE). I. INTRODUCTION AND LIFE HISTORIES OF PREDATORS OF SHORELINE SNAILS

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ABSTRACT

An overview of the taxonomic composition, geographic distribution, and general biology of the family Sciomyzidae is presented. Literature dealing with the taxonomy and biology of the genus *Tetanocera* is summarized, and collecting, rearing, and preservation techniques are discussed.

The natural histories, life cycles, and larval feeding habits of *Tetanocera fuscinervis* and *T. silvatica,* two species that prey on pulmonate snails occurring on wet shorelines, are presented.

INTRODUCTION

The acalyptrate Diptera family Sciomyzidae has a worldwide distribution and contains some 60 genera and 550 species (Knutson, 1987). The fauna of America north of Mexico consists of 21 genera and at least 175 species (Knutson et al., 1986). The biology of the family has been the focus of intensive study for over 40 years with the original impetus coming from the discovery of the snail-feeding habits of six species (Berg, 1953). Subsequently, numerous workers have described the immature stages and discussed the life histories, ecologies, and larval feeding habits of members of the family. Information is now available for over 200 species in the world, with particular attention to species occurring in the holarctic region. Larvae have been shown to prey on pulmonate aquatic snails, shoreline-inhabiting snails, terrestrial snails, snail eggs, slugs, and fingernail clams. Literature published before 1950 on the biology of Sciomyzidae has been discussed by Berg (1953) and Foote (1959). Berg (1961), Berg and Knutson (1978), and Knutson (1987) have summarized more recent findings.

The genus *Tetanocera* has a holarctic distribution and contains some 40 species, with 30 species being recorded from the Nearctic region (Knutson, 1987). Keys and descriptions of the adults of species occurring in America north of Mexico are available in Steyskal (1959) and Orth and Fisher (1982).

The present paper presents observations on the geographic distributions, habitat preferences, life histories, and larval feeding habitats of *T. fuscinervis* (Zetterstedt) and *T. silvatica* Meigen, two holarctic species having larvae that prey on pulmonate hygrophilous snails occurring in shoreline habitats. Subsequent papers will cover the biologies of species belonging to other trophic guilds, describe immature stages, and present a key to the third-instar larvae of the Nearctic species of *Tetanocera.*

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REVIEW OF LITERATURE

The relatively few papers that have focused on the natural histories and larval feeding habits and/or described the immature stages of species of *Tetanocera* are discussed below.

Dufour (1849) apparently was the first worker to study the biology of a species of *Tetanocera.* He encountered a larva of *T. ferruginea* Fallén in mid-November, 1846, in floating mats of duckweed (*Lemna* sp.) and water-starwort (*Callitriche* sp.) in a small pond near Saint-Sever, France. This larva completed development in the laboratory and produced an adult on April 26, 1847. Dufour never observed larval feeding but did describe and illustrate the third-instar larva and puparium.

Grünberg (1910) described the habitat of the larvae of *T. ferruginea* in Europe as being among such aquatic plants as *Lemna* and *Callitriche* in slow-flowing water. He reported that pupae overwinter and that there are probably two or more generations a year.

Brocher (1913) illustrated a larva of *Tetanocera* and stated that it resembled larvae of another sciomyzid genus, *Sepedon,* except that it was smaller and had much shorter lobes around the posterior spiracular disc. He reported that the larva left the water before forming a puparium and that the puparium did not float. Apparently, interspiracular processes (float hairs) were absent, but it is impossible to tell from his overly stylized drawing which species was involved.

Lundbeck (1923) discovered floating puparia of 26 species of Sciomyzidae, including *T. elata* Fabricius, *T. ferruginea,* and *T. silvatica,* in marshes and ponds in Denmark during the spring months. He made no observations of the larvae, and his comment that "the larvae are phytophagous or feed on decaying vegetable matter, perhaps also being carnivorous on small objects . . ." is unfounded. Lundbeck reared parasitoids belonging to a species of Ichneumonidae (subfamily Cryptinae) and wingless species of Proctotrupidae (Hymenoptera) from puparia of *T. ferruginea.*

Johannsen (1935) described but did not illustrate the puparium of *T. ferruginea* from material collected amid vegetation along the margin of a shallow pond near Ithaca, New York. He noted the appearance of the anterior spiracles, and described the posterior spiracular disc and perianal pad (anal plate). He reported that the puparium of this species differed from those of species of *Dictya* in the appearance of the posterior spiracular disc and the length/width ratio of the perianal pad.

Bhatia and Keilin (1937) described in considerable detail the larva of an undetermined species of Sciomyzidae that was obtained from a living land snail, *Vertigo genesii* Gredler, in England. They observed swallowing of air by the larva, a common sciomyzid habit, and noted that the larva imbedded itself in the prey snail until only the posterior spiracles were visible in the aperture of the shell. Their descriptions and drawings indicate that the larva was a member of the tribe Tetanocerini. The mouthhooks possessed four accessory teeth, the number usually found in larvae of *Tetanocera,* and the rows of "sensory papillae" found on the venter of each abdominal segment are recognizable in a few species of *Tetanocera.* However, the presence of only five finger-like lobes (=papillae) on the anterior spiracles illustrated is a character not known for any *Tetanocera* larva.

Berg (1953) made observations on *T. ferruginea, T. fuscinervis* (as *unicolor* Loew), and *T. rotundicornis* Loew. Larvae of the first species were free living and preyed on aquatic and shoreline snails. Newly hatched larvae of *T. fuscinervis* fed on pieces of a freshly killed *Helisoma* (Planorbidae), but died while still a

first instar. An adult of *T. rotundicornis* was reared from a larva that had infested a species of *Oxyloma* (Succineidae). He also presented evidence that overwintering occurred as pupae in *T. ferruginea* and *T. rotundicornis.* In a later paper, Berg (1961) summarized the larval feeding habits and morphology of the immature stages of 84 species of Sciomyzidae, including 16 species of *Tetanocera.*

Nielsen et al. (1954) discovered larvae of *T. robusta* Loew in wet areas in Iceland and suggested that the winter was passed as a pupa. They described and illustrated the third-instar larva.

Soós (1958) attempted to determine the number of generations produced each year for a variety of European species of Sciomyzidae by using data available on pinned specimens in museum collections. He reported that *T. arrogans* Meigen, *T. hyalipennis* Roser, and *T. silvatica* were bivoltine; whereas *T. punctifrons* Rondani and *T. fuscinervis* were univoltine. More recently, Berg et al. (1982) reported on seasonality, overwintering habits, and voltinism in north-temperate Sciomyzidae. Species of *Tetanocera* were represented in three of the five distinct groups which they recognized.

Berg and Neff (1959) discussed the use of larvae of certain predatory sciomyzids, including some species of *Tetanocera,* as biocontrol agents of aquatic snails serving as intermediate hosts of schistosome flukes that cause Schistosomiasis in man.

Foote (1961) discussed the life histories of 18 Nearctic species of *Tetanocera* and described and illustrated the eggs, larvae, and puparia of 12 species.

Disney (1964) reported that larvae of *T. ferruginea* were predators of pulmonate aquatic snails and described the larval habitat in England. He also recorded the ichneumonid wasp, *Phygadeuon elegans* Marshall, as a parasitoid of the pupa.

Rozkošny (1965) described and illustrated the mature larva and puparium of *T. ferruginea* and the puparia of *T. arrogans* and *T. elata.* Later, Rozkošny (1967) discussed the biology and larval feeding habits of several European species of Sciomyzidae, including *T. arrogans, T. elata,* and *T. ferruginea.* He also described and illustrated the eggs, mature larvae, and puparia of these species.

Although Foote (1963) briefly covered the slug-killing habits of two Nearctic species, *T. plebeja* Loew and *T. valida* Loew, the first detailed discussion of slug-killing habits in the genus was presented by Knutson et al. (1965). They presented information on the geographic distribution, habitat occurrence, life history, and larval feeding habits of *T. elata,* a Palearctic species. Other papers that discuss the biology of slug-killing species of *Tetanocera* are those of Trelka and Foote (1970) and Trelka and Berg (1977).

Knutson (1963) did an extensive literature review of sciomyzid biology and taxonomy, gave detailed information on the natural history of 26 species of nine genera occurring in the Palearctic region, described the larvae and/or puparia of 18 species, and presented a key to the mature larvae and puparia of 19 species. He included information on seven species of European *Tetanocera.* Later, Knutson (1970) summarized the natural history of sciomyzid flies occurring in Sweden, including notes on 11 species of *Tetanocera.*

Rozkošny (1966) summarized biological, ecological, distributional, and taxonomic information on the snail-killing flies of Czechoslovakia, including discussions of ten species of *Tetanocera.*

Beaver (1972) discussed the life histories and larval feeding habits of eight species of *Tetanocera* occurring in England, including four species that also occur in North America. She reported that *T. fuscinervis* and *T. silvatica* had larvae that

preyed on shoreline snails, whereas larvae of *T. ferruginea* and *T. robusta* attacked aquatic snails. Beaver (1973) presented ovipositional data for six European species, and later (1974*a,* 1974*b*) discussed intra-(four spp.) and interspecific (five spp.) competition in *Tetanocera.*

Berg and Knutson (1978) reviewed the basic biology of sciomyzid flies, recognizing eight trophic guilds in the family based on the feeding habits of the larvae.

Gasc et al. (1984) described and illustrated the chorionic stucture of the egg of *T. ferruginea,* suggesting that the chorion served as a plastron in eggs that are deposited in habitats that are subject to immersion. As a result, embryonic development can continue even if eggs are completely immersed.

Vala and Haab (1984) investigated the role of temperature and photoperiod in the development of *T. ferruginea* and the induction of pupal diapause. Manguin et al. (1985, 1988*a,* 1988*b*) and Manguin and Vala (1989) investigated the predatory behavior of *T. ferruginea* with respect to its foraging strategy, prey preferences, and the influence of snail biomass on numbers of prey consumed. Manguin (1989) demonstrated sexual dimorphism in puparia and adults of *T. ferruginea,* noting that the sex of the adult could be predicted quite reliably by measuring the body length of the puparium.

Vala and Gasc (1988) attempted to correlate the structure of the posterior spiracular disc of sciomyzid larvae with their habitat preferences. They suggested that well-developed interspiracular processes (float hairs) and elongated peripheral lobes typified the aquatic predators, whereas these processes and lobes are greatly reduced in the more terrestrial species.

Ferrar (1987*a,* 1987*b*) summarized knowledge of the biology and immature stages of the family Sciomyzidae, including several species of *Tetanocera.*

Materials and Methods

To avoid morphological descriptions and biological observations that may reflect pecularities of local races, species of *Tetanocera* were reared from as many different geographic localities as possible. Rearings were initiated from material collected in Alaska, Colorado, Idaho, Montana, New York, Ohio, and Washington. Adults collected with a standard insect sweep net were placed in 8-dram shell vials and transported alive to the laboratory. Larvae of aquatic species in shallow-water habitats were found by submerging floating and emergent vegetation and allowing the larvae and puparia to float free. Many puparia were also found by searching through floating or stranded debris. Larvae of shoreline and terrestrial species were obtained by confining large numbers of field-collected snails and slugs in shallow plastic pans for at least ten days. The pans had a substrate of moist paper toweling and were covered by cheesecloth held in place by rubber bands. The pans were examined daily for dead and dying host individuals and for larvae and puparia. Snails that appeared to be infested were isolated in small petri dishes containing moist, shredded peat moss and examined daily for larvae.

Rearings were maintained in large, well-lighted laboratories under room temperature conditions. Although relative humidities varied considerably in the laboratories, all rearings were held in small containers in which high humidities were maintained. Adults were confined in glass or plastic jars that were approximately 9.0 by 5.0 cm. The jars were covered with cheesecloth or fine screening and had a substrate of moist peat moss. Short lengths of cattail or short pieces of grass

served as resting sites for the adult flies. Small living snails or slugs were placed in each jar and a small pellet of a pasty mixture of honey and brewers' yeast was appressed to the wall. In additional to the honey/yeast pellet, crushed snails were added to provide a protein source for the flies.

Breeding jars were examined daily for eggs. These were removed with a fine camel's hair brush and transferred to plastic petri dishes, with each dish receiving ten to 20 eggs. Eggs of terrestrial *Tetanocera* were placed on moist peat moss, and those of the more aquatic species were placed on short lengths of microscope slides floating in a small amount of water. Samples of eggs of each species were preserved in 10% formalin.

When eggs of the aquatic species began to hatch, several small snails (under 5.0 mm) were added to the dishes. Dead snails were removed as they appeared and then replaced with living individuals. Cast exuviae were removed when produced and preserved in 70% ethanol. Larvae of all three instars were killed in hot water and preserved in 70% ethanol. As puparia were formed, they were transferred to 8-dram shell vials containing a layer of moist peat moss and a cap of cheesecloth or fine screening.

Most external structures of the larvae were examined without dissection, but the anterior spiracles were removed and mounted on microscope slides for detailed study. The anterior spiracles were macerated for 24 hr in a 10% solution of potassium hydroxide, rinsed in acid alcohol, dehydrated in a graded series of alcohol baths, and finally mounted on microscope slides in Canada Balsam or Permount. Cephalopharyngeal skeletons were recovered from cast exuviae, dissected out of preserved larvae, or removed from puparia. The skeletons were treated as described above and either mounted on microscope slides or studied directly in 70% ethanol by use of a dissecting microscope.

All measurements were made with an American Optical Company ocular micrometer that had been calibrated with a stage micrometer. Drawings of eggs and larval structures were made by using an ocular grid of equal squares. Preliminary sketches were made on white paper that had been similarly gridded into equal-sized squares. Final drawings were made either on Strathmore drawing paper or on No. 1½ Ross stipple board.

LIFE HISTORY STUDIES

Tetanocera fuscinervis (Zetterstedt), 1838; Insecta Lapponica Descripta: 737

Tetanocera fuscinervis is holarctic, occurring in Europe and Siberia as well as in North America. In the Nearctic region (Fig. 1), it is recorded from Newfoundland west to Alaska, and south to New York, Iowa, and Arizona (Knutson et al., 1986). Earlier American literature (e.g., Steyskal, 1959) referred to this species as *T. unicolor* Loew, 1847.

In central New York, adults and puparia were found only in stands of emergent vegetation growing at the south end of the White Church Marsh located south of Ithaca. Adults were swept from a borrow pit bordering the abandoned railroad as well as along the south shore of the main marsh. Puparia were taken most abundantly floating amid the emergent sedges in the borrow pit. In northeastern Ohio, adults were taken only in an unshaded fen located in the Herrick Preserve in Portage County. In Colorado (three localities near Florissant in Teller County), Idaho (several localities in the northern half of the state), and Alaska (the Matanuska Valley and south of Anchorage), adults were collected in open or partially

Fig. 1.—Distribution of *Tetanocera fuscinervis* in North America.

shaded marshes containing little water but supporting dense stands of emergent vegetation, especially species of *Carex*.

This species was used in the first attempt to initiate a rearing of any sciomyzid by confining wild-caught flies for oviposition (Berg, 1953). Adults of *T. fusci-*

nervis (=*T. unicolor*) collected by Berg in an unshaded grass-sedge marsh five miles south of Anchorage, Alaska, on July 2, 1952, were confined in an experimental model of what has now evolved as a standard breeding jar. They mated soon after confinement and laid eggs on July 3 and 4, attaching them to damp sphagnum moss at the bottom of the container. Although motion inside the egg membranes was noticed on July 8, no hatching occurred on that day nor on the next. Some eggs had hatched by the morning of July 10; all, by noon of July 11. As there was then no knowledge that the minute first-instar larvae attack and kill living snails, they were offered pieces of freshly killed and chopped *Helisoma subcrenatum* (Carpenter). They fed sparingly and showed little evidence of development. Although the larvae survived well (up to 14 days), all died without molting into the second instar (Berg, 1953).

Rearings were initiated by the present author from puparia taken at the White Church Marsh during March and April 1956 and from adults taken in June and early July 1958–60 in a small, partially shaded marsh located eight miles north of Sandpoint, Bonner County, Idaho (see Foote, 1961:148 for description of the Idaho site). Another rearing was initiated from adults collected on July 24, 1993, in an open grass–sedge marsh located one mile west of Florissant, Colorado.

Many eggs were obtained from laboratory-reared and wild-caught females. On March 14, 1956, two females and a male that had emerged on March 13 were placed in a breeding jar. Mating was noticed first on March 19 and was seen frequently thereafter. Females began ovipositing on March 21, but laid only 16 eggs before dying on March 23. Another laboratory-reared female deposited 33 eggs between June 21 and July 1, 1958. Each of the females collected in nature in Idaho during June and early July produced between 70 and 204 eggs during periods ranging from eight to 13 days. Colorado-reared adults lived in the breeding jars from three to 21 days but did not oviposit.

In the breeding jars, eggs were placed low on the glass jars, within two centimeters of the moss, on projecting sprigs of moss, and on shells of living and dead snails. One female deposited 95 eggs on the jar, 66 on projecting bits of moss, and 34 on shells of living *Fossaria obrussa* (Say). Those placed on moss were closely clustered in amorphous masses containing up to 30 eggs each. Eggs laid on the sides of breeding jars were more scattered and usually did not touch each other. Another female laid 108 eggs on the jar, three on shells, and none on moss. Under laboratory conditions, the incubation period was four to six days in the specimens collected in New York and Idaho but seven days in those from Alaska (n = 79: New York, 10; Idaho, 57; Alaska, 12).

Larvae fed on small *Gyraulus parvus* (Say) and *Helisoma* spp. but developed more slowly than did other predaceous sciomyzid larvae reported in the literature. A larva that hatched on June 24 destroyed several small *Helisoma,* but did not molt into the second instar until July 1. Seven other larvae remained in the second instar for nine to 11 days. Very few larvae reached the second instar, only four attained the third instar, and none formed a puparium. The causes of this heavy mortality rate are unknown. Knutson (1963) reared larvae of a European strain of *T. fuscinervis* (as *T. unicolor*) from hatching to pupariation, and did not mention a high mortality rate. However, only one adult emerged from his 19 puparia, and the puparia that were dissected contained mummified or decaying bodies.

The 17 puparia found floating at the White Church Marsh from early March to April produced adults 11 to 16 days after being brought into the heated laboratory. Greatest emergence occurred in 11 to 12 days.

In central New York, the earliest seasonal record for adults is June 10; the latest, September 2. Adults were collected occasionally throughout the summer months. Puparia were taken from early March to early April. In northern Idaho, the earliest record for adults is June 1; the latest, August 11. Because of the comparatively slow growth of the larvae, *T. fuscinervis* may have only one generation per year. Overwintering evidently occurs in the pupal stage. Living puparia were collected on March 1 (more than three months before the earliest record for adults in this region) by breaking through the ice at the White Church Marsh.

Two of eight puparia collected on March 12 produced ichneumonid wasps of an undetermined species on March 24.

Tetanocera silvatica Meigen, 1830; Systematische Beschreibung der bekannten eüropaischen zweiflügeligen Insekten: 41.

Tetanocera silvatica is a holarctic species that has a transcontinental distribution in Canada and the northern United States (Knutson et al, 1986), ranging from Alaska to Newfoundland and south to Minnesota, Colorado, and Arizona (Fig. 2).

Adults of this species were most commonly encountered in permanent marshes or in marshy areas surrounding lakes. Other adults were taken in more temporary herbaceous wetlands, but none were encountered in wooded habitats. Near Florissant, Colorado, adults were taken on July 24, 1993, in association with *T. fuscinervis, Dictya montana* Steyskal, *Renocera johnsoni* Cresson, *Sepedon fuscipennis* Loew, and *Limnia sandovalensis* Fisher and Orth from a small (ca 1 acre), unshaded sedge marsh in which water levels had dropped noticeably as summer advanced. Adults of *T. silvatica* were especially common in somewhat drier, marginal areas of the marsh. In Banff National Park on August 10, four adults that served as the basis of a laboratory rearing were swept from herbaceous vegetation growing in a floodplain marsh partially shaded by spruces. Small pools of open water one-half to one meter deep were scattered across the marsh. Three third-instar larvae of *T. silvatica* were found in shoreline debris around the shallow pools. Small aquatic snails of the genera *Helisoma, Physella,* and *Gyraulus* were abundant, and several individuals were crawling over the wet shoreline bordering the pools. Amphibious snails of the genera *Catinella* and *Oxyloma* were abundant on the shoreline vegetation. Another indication that the larvae are usually associated with shoreline habitats was my failure to recover larvae from floating vegetation in western Alberta, central New York, northwestern Idaho, and central Colorado despite repeated attempts.

Numerous matings in the breeding jars were noted at various times during the day between 10:00 A.M. and 9:30 P.M. The male's position was similar to that observed in other species of the genus, except that his fore tarsi were placed close together on the middle of the female's frons rather than lying along her eye orbits. The first 24 eggs were obtained on August 16 from the two females collected in nature on August 10. Seven eggs were affixed close together on the umbilical surface of a dead *Helisoma,* two were on the shell of a dead *Lymnaea,* six were placed on peat moss near a living *Lymnaea,* and the remaining nine eggs were scattered over the glass walls of the jar. A total of 71 eggs was deposited by these two females between August 16 and September 5.

The incubation period lasted two to three days (n = 18), and newly hatched larvae were given small living *Gyraulus* and *Lymnaea* snails. As in *T. fuscinervis,* larval development in this species was somewhat prolonged, with the first stadium

Fig. 2.—Distribution of *Tetanocera silvatica* in North America.

lasting four to five days ($n = 6$). Another behavior that was somewhat unusual for species of *Tetanocera* was a tendency for the newly hatched larvae to feed gregariously within individual snails, with up to four larvae feeding together in a single *Gyraulus*. In contrast, second and third instars were more solitary in their

feeding habits and did not occur together in any one snail. The second stadium was completed in five to six days ($n = 3$), but no larva managed to pupariate. Another rearing initiated by two females collected on July 24 in the marsh near Florissant, Colorado, was somewhat more successful in that adults emerged from two puparia obtained in the laboratory rearing. As in the earlier rearing, the newly hatched larvae commonly fed gregariously in such snails as small species of *Gyraulus, Helisoma, Lymnaea,* and *Oxyloma,* whereas older larvae fed singly. Between six and eight snails were consumed by two larvae during feeding periods of 22 and 27 days, respectively. The first stadium lasted four to six days ($n = 3$); the second, five days ($n = 2$); and the third, ten to 11 days ($n = 2$). The pupal period for a female was 17 days, whereas that of a male was 21 days. Mating among these reared adults began within three days after emergence, but no eggs were deposited.

The earliest seasonal record for adults was obtained on May 20 (Minnesota); the latest, on August 17 (Alaska). Adults have been taken throughout the summer months in several localities, and it is probable that *T. silvatica* is at least bivoltine. The duration of the egg-to-egg period in the laboratory was 46 to 55 days, and there was no indication of diapause in any life stage.

Discussion

The habitat distribution of these two species of *Tetanocera* is quite similar in that both occur in open, largely unshaded herbaceous marshes with fluctuating water levels. More specifically, their larvae are associated with shorelines and can be found preying on stranded pulmonate aquatic and hygrophilic snails occurring in such situations. By frequenting shoreline habitats, the larvae probably escape competition from the more aquatic species of *Tetanocera* and other genera of Sciomyzidae. They probably do encounter competition from larvae belonging to other shoreline-dwelling genera of the family, such as species of *Pherbellia,* as well as from larvae of other species of *Tetanocera.* However, the specialization of the other species of shoreline *Tetanocera* on particular assemblages of gastropods probably mitigates interspecific competition within the genus. In contrast to such trophically specialized shoreline-dwelling species that prey on succineid snails (*T. melanostigma* Steyskal, *T. oxia* Steyskal, *T. rotundicornis*) or slugs (*T. plebeja*), larvae of *T. fuscinervis* and *T. silvatica* are rather generalized predators, frequently attacking stranded individuals of more aquatic species of Gastropoda.

Competition for a limiting resource (stranded aquatic snails) may occur occasionally between *T. fuscinervis* and *T. silvatica.* Adults of the two species commonly occur in the same marsh at the same time, although the first species usually is more abundant. For example, the acre-sized marsh near Florissant, Colorado, supported a large population of *T. fuscinervis,* but a relatively small population of *T. silvatica.* Perhaps biotic (enemies) and abiotic (weather conditions) factors maintain populations of one or both species of *Tetanocera* below the carrying capacity of the marsh habitat such that there is only rarely a shortage of larval food.

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This paper is dedicated to the memory of Dr. C. O. Berg, formerly of the Department of Entomology at Cornell University in Ithaca, New York.

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